

## VARIATION IN NATURAL MORTALITY: IMPLICATIONS FOR QUEEN CONCH STOCK ENHANCEMENT

*Allan W. Stoner and Robert A. Glazer*

### ABSTRACT

Our long-term investigations of mortality and predation in the large, economically significant gastropod *Strombus gigas* (queen conch) indicate that instantaneous rates of natural mortality ( $M$ ) in nursery grounds in the Bahamas and the Florida Keys are often higher and more variable than recognized earlier. Wide divergence from a simple size-specific curve of natural mortality was caused by seasonal, interannual, and site-specific sources of variation. In the Florida Keys, mortality rates for 200-mm conch were highest in summer and most stable in the fall, but summer values of  $M$  varied interannually from <2.0 to 12.0. Mortality rates for 100-mm conch, often considered ideal in size for field releases, varied from 0.5 to 12.0, depending on site, season, conch density, and deficits in behavior and shell form associated with hatchery rearing. Unlike many marine invertebrates, juvenile queen conch have an inverse density dependence in mortality. Because of the logarithmic relationship between mortality rate and the cost to enhance a stock, it is critical for those involved in stock enhancement to have a realistic understanding of mortality processes and effects and to optimize culture and release strategies for highest possible survival. Specific recommendations are made for queen conch releases.

One of the important premises of releasing hatchery-reared juveniles into the natural environment for stock enhancement is that high levels of natural mortality associated with the earliest stages of development are circumvented. Also, because mortality rates decrease rapidly as animals mature from larval to juvenile stages, variation in mortality during juvenile and adult stages is often assumed to be negligible. Although the first assumption is probably correct for most marine species, the second is not, and variation in mortality can have a large effect on yield (Vetter, 1988).

Success in releasing hatchery-reared marine species is usually gauged by the number of individuals that are recovered subsequent to release. The results have been highly variable, ranging from almost total mortality or loss of the released stock to rates of recovery approaching 100%. Temporal, spatial, and size-related variations in survivorship have been reported for abalone (Schiel, 1992), scallops (Tettelbach and Wenczel, 1993), queen conch (Stoner and Davis, 1994), and clams (Peterson et al., 1995). Future success in stock-enhancement programs will depend on the optimization of release protocols designed to achieve high survivorship rates and low cost per survivor.

The large gastropod *Strombus gigas* (queen conch) is one of the most important traditional fishery species in the greater Caribbean region, but the fishery has declined below the level of economic viability in several countries of the region, and serious declines have been reported in most others (Appeldoorn, 1994). Fishing for queen conch is now illegal in the continental United States, Bermuda, and Bonaire, but efforts to allow natural rebuilding of stocks through fishing moratoria have not been effective in Florida (Glazer and Berg, 1994; Berg and Glazer, 1995) or Bermuda (Berg et al., 1992). Stoner et al. (1996, 1997) concluded that reproductive stocks in the Florida Keys are now so low and larval supply to nursery grounds is so irregular that recruitment is below a critical level. For 20 yrs, release of hatchery-reared conch has been recommended as a way to replenish

depleted stocks (Berg, 1976; Weil and Laughlin, 1984; Davis et al., 1987). Culture techniques have been perfected through many years of research reviewed by Creswell (1994) and Davis (1994), but releases into the field have not been successful because of high rates of mortality (Jory and Iversen, 1983; Laughlin and Weil, 1983; Appeldoorn, 1985; Iversen et al., 1986; Stoner and Davis, 1994).

Queen conch provide a convenient model for studying natural mortality because the species is large and slow-moving, is easily tagged, and leaves a record of mortality in the form of empty or broken shells. Although conch occasionally die from low-temperature shock and high wave energy in Florida and the Bahamas (Iversen et al., 1986; Glazer, pers. obs.), we know of no record of their having diseases or parasites, and most postsettlement mortality appears to be predator-induced. Many new investigations on queen-conch mortality have been conducted over the past 10 yrs, and much of this work has been carried out at our laboratories in the Bahamas (Stoner) and Florida (Glazer). In the present paper we present a synopsis of the mortality estimates and experiments related to predator-induced mortality in queen conch. We pay particular attention to variation in mortality with respect to season, location, conch ontogeny, and density. Although the results of this study are specific to queen conch, the forms of variation in mortality that we identify are universal and need to be considered in any stock-enhancement program.

#### MATERIALS AND METHODS

This study is based on results from a variety of published and unpublished investigations. Appeldoorn (1988) summarized available mortality data for queen conch through the mid-1980s and produced the first curve of age-specific mortality for the species. New data on mortality in free-ranging juvenile queen conch are available for two geographic regions: near Lee Stocking Island in the Exuma Cays, Bahamas (Sandt and Stoner, 1993; Stoner and Ray, 1993; Stoner and Davis, 1994), and in the Florida Keys (Glazer, unpubl. data). We restrict our analysis to mortality data for free-ranging individuals, though several other studies of relative mortality in tethered juvenile queen conch are available for discussion (Marshall, 1992; Ray and Stoner, 1994, 1995a, b; Ray et al., 1994; Stoner and Lally, 1994).

The aging of wild conch is imprecise because they grow at different rates in different environments (Martín-Mora et al., 1995), and mortality appears to be more directly related to absolute size than to age (Ray et al., 1994). To compare our mortality rates with those cited in Appeldoorn's review (1988), we converted his age-specific data to a size-specific relationship using conch length information provided in the original publications cited (Fig. 1). Also, because queen conch cease to grow in shell length when they reach sexual maturity at approximately 3 yrs of age (Randall, 1964) and because we wanted our findings to be relevant to the stock-enhancement issue, we restricted our analysis to juvenile conch <225 mm in shell length and <3 yrs of age.

Our calculations for instantaneous rate of natural mortality ( $M$ ) were made on the basis of survivorship data and were standardized for an annual period as reported by Appeldoorn (1988) and as is common for fisheries data:

$$M = (\log_e n_1 - \log_e n_2) / y$$

where  $n_1$  and  $n_2$  are the numbers of individuals in the population at time 1 and at some subsequent time 2, and  $y$  is the fraction of a year between time 1 and 2. In most cases, calculations for  $M$  were made on the basis of relatively short periods of time (30–90 d, 0.07–0.25 yrs) because it was desirable to evaluate seasonal and other forms of variation within the animal's first 3 yrs of life.

**EXPERIMENTS IN THE BAHAMAS.**—Survivorship estimates in the studies of tagged conch near Lee Stocking Island (Sandt and Stoner, 1993; Stoner and Ray, 1993; Stoner and Davis, 1994) were

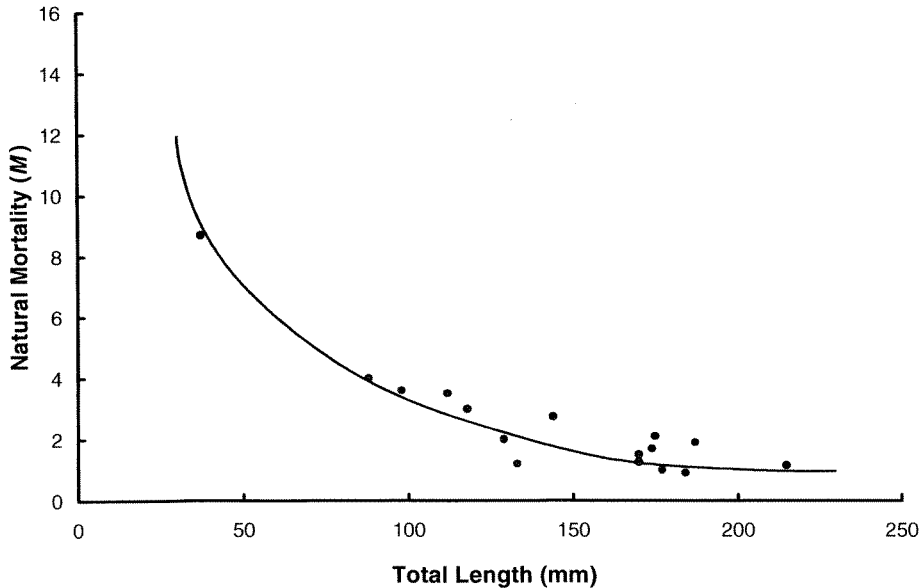


Figure 1. Instantaneous rates of natural mortality for juvenile queen conch. Adapted from Appeldoorn (1988).

based on exhaustive surveys that were repeated at regular intervals (1–3 mo) after the conch were released. In this analysis we have converted the survivorship data to values for  $M$ . Although the precise methods for the tag and recovery investigations and the population estimates, dates, and time intervals have already been reported in detail, we provide brief descriptions here.

In January 1989, Sandt and Stoner (1993) marked 500 small, wild conch (35–54 mm shell length) at a shallow, subtidal recruitment site near Lee Stocking Island. Thin spaghetti tags did not inhibit the normal burial activities of the small conch but could be detected by divers even when the conch were buried in the sediment. The tagged conch were surveyed every week for 6 wks; the mortality for the entire period is considered here.

Stoner and Ray (1993) tagged 500 wild, juvenile conch (90–112 mm shell length) and released them in approximately equal numbers in three locations within the Shark Rock nursery near Lee Stocking Island in September 1989. Releases were made near the center of an existing conch aggregation (Zone F), where mean density was 1.0 conch  $m^{-2}$  at the beginning of the experiment, and 0.5 km east (Zone B) and west (Zone I) of the primary aggregation. Exhaustive searches for the tagged conch were made 1, 4, 7, and 12 mo later, and the recovery rates were used to determine seasonal mortality rate.

Stoner and Davis (1994) conducted several experiments with wild and hatchery-reared conch near Lee Stocking Island. In March 1991, approximately 2500 wild conch and 2500 hatchery-reared conch, with an average shell length of 100 mm, were tagged and released in each of two large seagrass areas near Lee Stocking Island. Site C1 was in the middle of a traditional nursery ground, and site C2 was in an adjacent area with no conch within 300 m. Complete tag recoveries were conducted 2, 5, and 7 m after release. Stoner and Davis (1994) also examined survivorship and growth of conch in pens and on tethers, but only free-ranging conch are considered here.

**EXPERIMENTS IN THE FLORIDA KEYS.**—Tag-and-recapture studies were conducted at three nursery sites in the Florida Keys so that seasonal and long-term variations in the natural mortality of wild populations of juvenile queen conch could be examined. The nurseries, at Big Pine Key, Tingle's Island, and Walker's Island, were all located in nearshore hard-bottom habitats that were character-

ized by dense stands of red algae (order Ceramiales), sponges, octocorals, and infrequent patches of turtlegrass (*Thalassia testudinum*). At each site, water depth ranged from intertidal to 4 m. Both juvenile and adult conch were common at these three sites, and because the juveniles were large (mean = approximately 180 mm shell length), they were easy to survey. In all of these sites, divers tagged as many juvenile conch as possible and conducted seasonal recaptures (four times per year) between 1987 and 1993. Exhaustive surveys were made at the release sites and in the adjacent areas. Rates of survivorship were derived from abundance estimates determined by means of the Jolly-Seber tag-recapture model for open populations (Seber, 1982), and natural mortality rates were calculated as described earlier. In all cases, spring surveys were excluded from survivorship and mortality calculations because abundance estimates could be affected by spring recruitment to the observed population.

Tag-and-recovery experiments were also conducted with juvenile conch reared in the hatchery facility of the Florida Marine Research Institute. In the first experiment, begun in August 1993, two size-classes of tagged juveniles (mean = 51 mm shell length, SD = 6,  $n = 274$ ; mean = 79 mm, SD = 7,  $n = 120$ ) were released in equal numbers at two locations separated by 0.4 km at Walker's Island. At release, the density of wild juvenile conch at Walker's Island was 27.9 conch  $m^{-2}$ . Exhaustive searches for the conch were made three times per week for 1 mo after their release, and mortality was calculated for the overall period. A second experiment was conducted at Walker's Island in spring 1994. In April, 616 conch (56 mm, SD = 10) were tagged and released in equal numbers at two sites and monitored for 1 mo as before.

A third release of hatchery-reared conch was made at Delta Shoal in April 1996. This nursery site is located on a shallow platform approximately 8 km offshore from Key Vaca in a turtlegrass meadow with moderate shoot density and a sandy substratum. Water depth is 5 m. Hatchery-reared conch in two size-classes (mean = 60 mm, SD = 7; 80 mm, SD = 10) ( $n = 160$  each) were released in equal numbers at two sites separated by 150 m at Delta Shoal. The conch were marked with aluminum tags, and they were recovered once per week through 23 June by divers using underwater metal detectors tuned specifically for the tags (Glazer et al., in press). In this experiment, mortality was calculated for the 2-mo period according to the method of Jackson (1939) as adapted for this experiment (Glazer et al., in press) to compensate for emigration.

## RESULTS

**VARIATION FROM THE PREDICTED SIZE-SPECIFIC CURVE.**—All mortality data used in Appeldoorn's (1988) review were for wild queen conch 80–215 mm total shell length, except for one value for small, hatchery-reared juveniles (approximately 40 mm) (Fig. 1). The hypothetical curve shows a rapid decline in mortality rates for conch between 40 and 80 mm and then a slow decrease in  $M$  (from 4.0 to 1.0) with increasing conch size.

Two important observations can be made when our new mortality values are added to the earlier data and curve (Fig. 2). First, instantaneous rates of mortality estimated from survivorship data gathered over relatively short periods (1–3 mo) can be very high, even for large conch near sexual maturity ( $> 200$  mm). Second, variation in mortality rates was very large throughout the range of sizes examined (40–225 mm). The only new estimate of  $M$  for wild conch as small as 45 mm in shell length was 12.0 (from Sandt and Stoner, 1993), well above that found on the mortality curve generated by Appeldoorn (1988). Other data for conch near 50 mm are for hatchery-reared animals in the Florida Keys; these fell above and below Appeldoorn's mortality curve (Fig. 2).

**TEMPORAL VARIATION IN MORTALITY.**—Long-term data from three conch nurseries in the Florida Keys (Fig. 3) show dramatic changes in the mortality rates of large juveniles over time, on both seasonal and interannual scales. When data for two or more seasons were

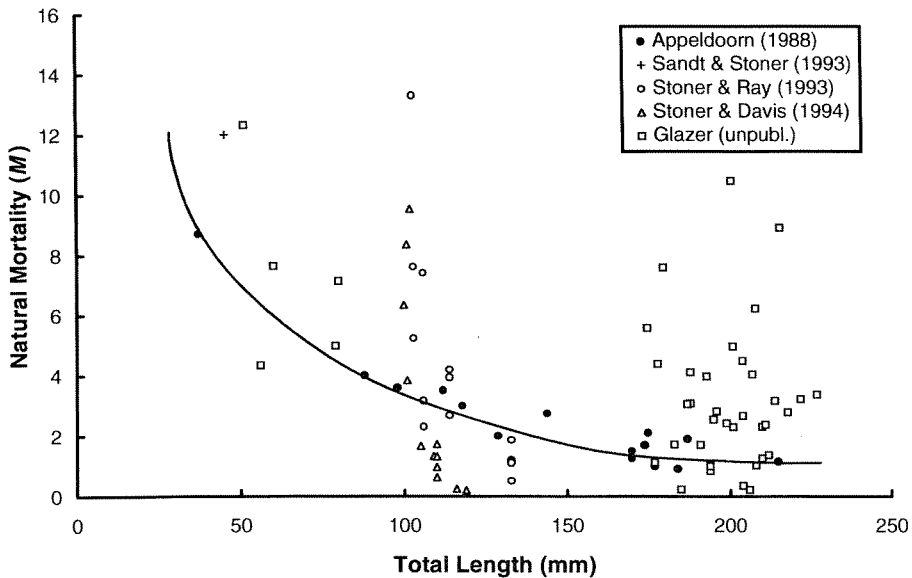


Figure 2. Instantaneous rates of natural mortality for juvenile queen conch. Data collected subsequent to Appeldoorn's (1988) analysis have been added to the points and curve shown in Figure 1. All of the data are from studies of mortality in free-ranging conch.

available for a particular year, mortality rates were always highest during summer months at Big Pine Key. At the other nurseries, summer mortalities were either high or close to the values determined for the other seasons, particularly when overall mortality rates were low. An exception occurred at Walker's Island in 1992, when summer and winter mortalities were about one-half the fall value.

Interannual variation was particularly apparent at Big Pine Key, mortality rates were high in 1988 and 1990, and values in 1989 were well below the mean calculated over all dates (4.71). In areas where data were collected during the same seasons at Big Pine Key and at Tingle's Island, mortality rates were relatively similar (Fig. 3). Mortalities at Walker's Island were the most stable, varying between approximately 1.0 and 4.0 over 7 yr except in summer 1988. It should be noted, however, that even this range of variation in  $M$  represents more than an order-of-magnitude difference in the percentage of conch surviving, from 36.8% per year down to 1.8%. Over the 7-yr investigation, rates of mortality were least variable in the fall.

**INTERACTIONS OF TIME, SIZE, AND DENSITY.**—The effect of season on conch mortality was obviously modified by the effect of increasing conch size in the Shark Rock nursery near Lee Stocking Island (Fig. 4). As conch grew from an average length of 103 to 133 mm, they appear to have escaped the normally high mortality rates associated with summer months observed in Florida. A high correlation coefficient was observed between  $\log_{10}$ -transformed values of  $M$  and conch length ( $r = 0.833$ ,  $F_{1,10} = 22.73$ ,  $P = 0.001$ ), despite the obvious differences in mortality among zones in the nursery (Fig. 4).

Conch mortality rates were always lowest in the center of the Shark Rock nursery (Zone F), whereas they were high in peripheral zones B and I. Although simple locational effects on mortality cannot be ruled out, differences in conch density provide the most

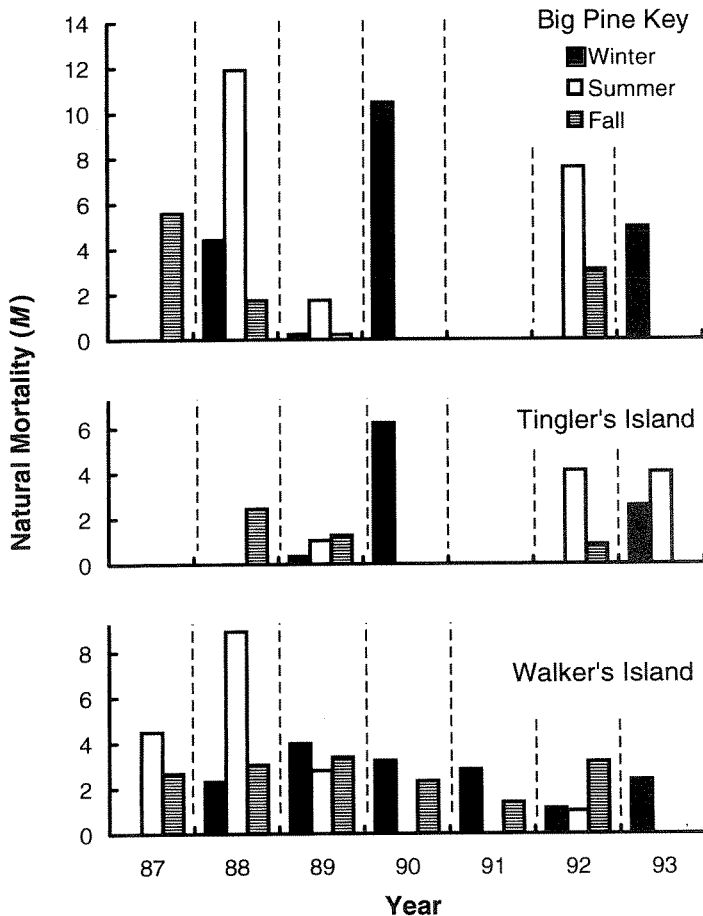


Figure 3. Instantaneous rates of natural mortality for large juvenile queen conch (175–215 mm shell length) shown over time for three different nurseries in the Florida Keys. Data for three seasons are shown. Note that missing histograms indicate no data, not zero mortality.

plausible explanation for differences in mortality rates among the zones. Average densities in Zones B and I were low (0.18 and 0.1 conch  $m^{-2}$ , respectively) compared to the density in Zone F (1.15 conch  $m^{-2}$ ).

Mean length of conch in the Florida nurseries was always 175–215 mm. Variation in the mortality rates (Fig. 3) of these large conch was not readily explained by differences in size or density. Even when data for the three different nursery grounds were examined independently, there were no significant correlations between mortality and mean size ( $r < 0.33$ ,  $P > 0.2$ , for all sites) or between mortality and conch density ( $r < 0.47$ ,  $P > 0.40$ , for all sites).

**PERFORMANCE OF HATCHERY-REARED CONCH.**—Mortality rates of hatchery-reared conch were consistently higher than those of wild conch at two adjacent sites near Lee Stocking Island, regardless of season (Fig. 5). None of the interaction terms in a 3-way ANOVA were significant ( $P > 0.10$  in all cases), and differences in mortality between the two sites

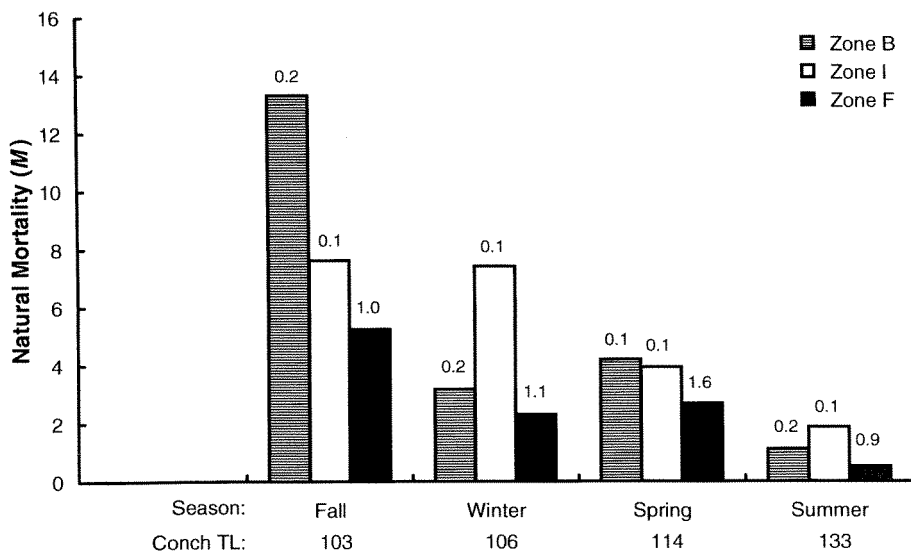


Figure 4. Instantaneous rates of natural mortality for juvenile queen conch in three zones of the Shark Rock nursery ground, Lee Stocking Island, Bahamas. Zone F was in the center of the nursery. Zones B and I were on the periphery, where densities of juvenile conch (shown above the histograms) were low. Average total lengths (TL) of tagged conch reflect growth over the study period from fall 1989 through summer 1990.

were not significant ( $F_{1,3} = 1.93$ ,  $P = 0.26$ ). However, differences among the seasons and between the conch types were highly significant ( $F_{2,3} = 408.1$ ,  $P = 0.002$ , and  $F_{1,3} = 15.43$ ,  $P = 0.029$ , respectively). Hatchery-reared conch were killed at rates 1.5–6.4 times higher than were wild conch. Wild conch grew faster and had consistently lower mortality rates than did hatchery-reared conch over the 7-mo experiment (Fig. 5).

Small hatchery-reared conch were released in several experiments in the Florida Keys between 1993 and 1996. Despite a very high ambient density of young conch at Walker's Island in 1993, mortality rates were high:  $M$  was between 5 and 12.3 for 79- and 51-mm conch, respectively (Table 1). Mortality rates for 56- to 80-mm conch in 1994 and 1996 were always high, between 4.3 and 7.7. Although the lower values for  $M$  are close to the mortality rates predicted by Appeldoorn (1988) (Fig. 1), most are much higher.

## DISCUSSION

**SOURCES OF VARIATION IN MORTALITY.**—Reviews of mortality rates for fishes (Vetter, 1988) and motile molluscs such as scallops (Orensanz et al., 1991) and abalone (Shepherd and Breen, 1992) show that age- and size-specific data are relatively rare. However, existing data usually show a decrease in natural mortality rate with increasing age or size (e.g., Whetstone and Eversole, 1978; Saito, 1984; Shepherd and Breen, 1992; Peterson et al., 1995), as is generally assumed. Field experiments using 10 size classes of juvenile queen conch (20–130 mm shell length) at a single site in the Bahamas indicated that there was a smooth sigmoid increase in survivorship as conch size increased (Ray et al., 1994). However, when all of the available data on mortality of free-ranging juvenile queen conch were considered together, it was impossible to fit any size-specific curve (Fig. 2), and it is

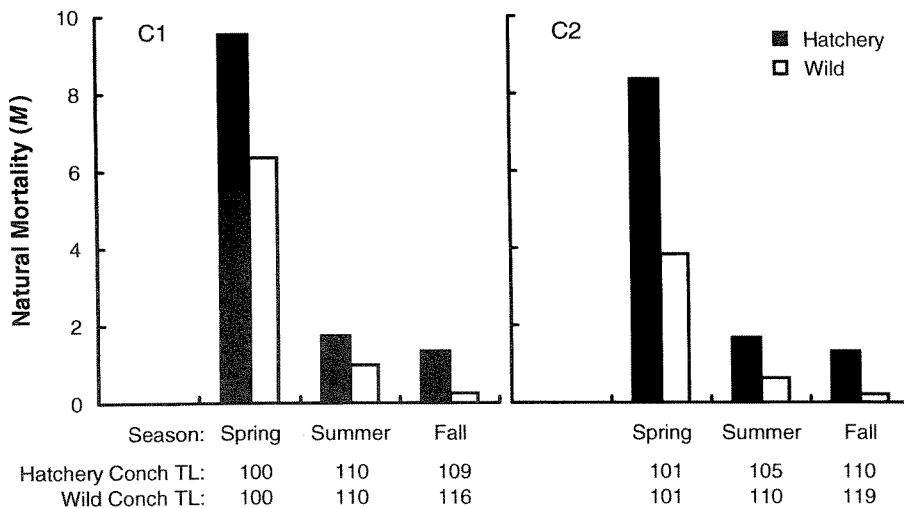


Figure 5. Instantaneous rates of natural mortality in hatchery-reared and wild conch at two study sites near Lee Stocking Island, Bahamas. Site C1 was within the boundaries of a juvenile aggregation. Site C2 was outside the aggregation, 300 m away. Average lengths of tagged conch reflect growth over the study period from March through November 1991.

clear that size-dependent mortality can be completely masked by variations in time and space.

Mortality in juvenile queen conch varied seasonally and interannually. Although the seasonal pattern is still not absolutely clear because of confounding variables, summer mortality rates were consistently high for large juveniles in the Florida Keys. This result is not surprising given that high summer temperatures probably accelerate metabolic, locomotor, and feeding rates of fish and invertebrate predators. In the Bahamas and Florida, an important predator of juvenile conch is the tulip snail (*Fasciolaria tulipa*). This predaceous snail appears to be most active during summer months (pers. obs.), and Jory (1982) showed that predation rates on queen conch juveniles are directly related to water temperature. Also, certain predators may be more abundant in conch nurseries during particular seasons or years, but we know of no quantitative data concerning these predators that would be adequate for determining seasonal abundance patterns. Peterson et al. (1995) concluded that the late fall and winter were the best times to release hard clams (*Mercenaria mercenaria*) into the wild because their primary predators (*Callinectes sapidus*) were relatively dormant during that time. The same strategy may be appropriate for conch, but given that conch of different sizes are consumed by different types of predators, from xanthid crabs feeding on newly settled conch (Ray et al., in review) to sea turtles that consume large juveniles and adults, temporal variation in mortality may be strongly confounded by conch size.

Although juvenile queen conch live in very specific locations within large, seemingly homogeneous seagrass beds in the Bahamas (Stoner et al., 1994), mortality rates were very different in different regions of the Shark Rock nursery. This variation appears to have been related to differences in conch density; natural mortality decreases with in-



Table 1. Instantaneous rates of natural mortality ( $M$ ) for hatchery-reared juvenile queen conch released at two sites in the Florida Keys. Mortality rates are based on tag-and-recovery experiments conducted with free-ranging conch.

Site	Date	Mean length (mm)	$M$
Walker's Island	summer 1993	51	12.31
	summer 1993	79	4.99
	spring 1994	56	4.34
Delta Shoal	spring 1996	60	7.63
	spring 1996	80	7.13

creasing density. A similar conclusion of inversely density-dependent mortality in juvenile queen conch has emerged from tethering experiments (Marshall, 1992; Ray and Stoner, 1994, 1995a). A weak reverse trend (density-dependent mortality) was reported for the abalone *Haliotis laevis* (Shepherd and Breen, 1992). Understanding the relationships between density and mortality in target species will be particularly critical in stock enhancement, and it is unlikely that the relationships are linear. Field experiments have shown that juvenile queen conch compromise growth rate by maintaining aggregations of relatively high density, but mortality was inversely density dependent and aggregation behavior confers survivorship advantage on the population (Ray and Stoner, 1995b).

Other variables that may affect spatial variation in mortality rates include the amount of vegetative cover (Marshall, 1992; Ray and Stoner, 1995b), water depth, abundance and types of predators, and even the degree of fishing pressure on predators such as lobsters or sea turtles. On the basis of temporal and spatial variations in mortality, Tettelbach and Wenczel (1993) hypothesized that enhancement of bay scallops (*Argopecten irradians*) would be most successful if scallops were released at several different locations. Spatial variation in mortality of the abalone *Haliotis iris* was also highly significant, but Schiel (1993) concluded that commercial-scale enhancement could be economically practical even if low mortality occurred in only some of the release sites. The effects of scale and stocking density on conch mortality have not yet been investigated but should be considered in the development of optimal stock-enhancement strategies. For example, 1000 conch released at one individual per square meter may result in a mortality rate very different from that of 10,000 released at a similar density.

POTENTIAL EFFECTS OF HATCHERY REARING.—Despite the difficulties involved in hatchery production of queen conch, the culture of this species has become relatively routine in a small number of facilities in the greater Caribbean region. Hatchery-produced animals, however, can have certain morphological, physiological, and behavioral deficiencies that increase their mortality in the field over that of natural stocks. Quantitative estimates of these differences between wild and hatchery-produced animals are few but have been made for the trout *Salmo trutta* (Berg and Jorgensen, 1991), the abalone *Haliotis iris* (Schiel, 1992) (Table 2), and queen conch (Stoner, 1994). Although the mechanisms are not clear, hatchery-reared animals suffered significantly higher mortality rates than wild animals did in all of these cases. Tagging and other handling procedures were equivalent. Olla et al. (1994) concluded that deficiencies in social behavior and predator-avoidance could have substantial influence on survivorship capabilities in hatchery-reared fishes, even in the absence of any morphological deficiencies. Stoner and Davis (1994) found that hatchery-reared queen conch had a lower rate of burial into the substratum than wild

Table 2. Values collected from the literature on the instantaneous rates of natural mortality ( $M$ ) for selected molluscs. Emphasis has been placed on mortality values calculated for free-ranging, unprotected juveniles observed for periods of 1 yr or less. (100) indicates total mortality over the study period.

Taxon	Reference	$M$ (year <sup>-1</sup> )	Comment
<b>Abalone</b>			
<i>Haliotis discus</i>	Saito (1984)*	10.3	<22 mm, hatchery-reared
		4.71	>22 mm, hatchery-reared
<i>H. iris</i>	Schiel (1992)	8.66	0+ year class, hatchery-reared
		4.07	0+ year class, wild
		21.77	1+ year class, hatchery-reared
		3.37	1+ year class, wild
	Schiel (1993)	0.32–4.44	3–0 mm, hatchery-reared
<i>H. kamtschatkana</i>	Emmett and Jamieson (1988)	0.44–1.52	80–90 mm, wild
<i>H. laevigata</i>	Shepherd (1987)*	3.5–4.6	settlement to 6 mo, wild
		0.2–1.1	0.5–2.5 yrs, wild
<i>H. rubra</i>	McShane (1990)	6.6–10.2	settlement to 5 mo, wild
	Day and Leorke (1986)*	0.91	6–18 mo, wild
<i>H. scalaris</i>	Shepherd and Godoy (1989)*	1.1	1–3 yrs, wild
<b>Bivalves</b>			
<i>Mercenaria mercenaria</i>	Whetstone and Eversole (1978)*	5.0	13 mm
		1.0	20 mm
		0.3	27 mm
	Flagg and Malouf (1983)*	3.42–(100)	3 mm, 10–11 mo
		0.05–3.07	23 mm
	Peterson et al. (1995)*	0.81–3.25	0+ yr class, habitat-dependent
<i>Argopecten irradians</i>	Tettelbach and Wenczel (1993)*	0.60–(100)	15–40 mm, hatchery-reared, few survivors

\* Values for  $M$  that were calculated from reports of survivorship and time interval between surveys.

\* Values extracted from Shepherd and Breen (1992).

conch did, in addition to having shorter apical spines on the shells. Both of these factors could affect the higher mortality rates observed in the cultured conch. Successful stock enhancement will depend upon releasing animals that have mortality rates comparable to those of natural stocks.

**RECOMMENDATIONS FOR RELEASING HATCHERY-REARED CONCH.**—The average mortality rate for juvenile queen conch may be close to the size- or age-specific equation postulated by Appeldoorn (1988), but variation over space and time (weeks to years) can be very large because of the variables that we have identified. Releasing conch at the wrong time or place could have serious consequences. On the basis of this review of mortality and our general experience with queen conch in the field, we make the following recommendations:

(1) Queen conch should be released at the largest size practical, probably >70 mm shell length, but the advantage of size can be lost if a low-quality seed stock is used or if the site selected or the release technique is poor.

(2) All effort should be made to increase the quality of seed animals. High-quality seed animals have shell characteristics (e.g., shell shape and thickness) that are normal, growth rates that are as high as those found in wild populations, and the behavioral patterns needed to avoid predators and to detect and consume appropriate foods.

(3) Site selection for stock enhancement should be made on the basis of preliminary information. First, if possible, historically important nursery areas (i.e., areas occupied by conch or areas known to have been previously occupied) should be used rather than sites that are simply convenient or seem to have suitable substrata. We now know that nurseries occur in very specific locations for a variety of reasons, including low predation rates, but historically important nurseries may have changed over time because of natural events or human activities. In addition, distributional information may not be available for these nurseries. In such cases, preliminary experiments on the trophic suitability of the habitat for young conch will be needed. These should include small-scale transplant experiments (normally using enclosures) and experiments on predation rate (Stoner, 1994). Cultured conch are usually too expensive for trial-and-error releases.

(4) Because mortality appears to vary interannually, losses may be unpredictable even in a well-studied nursery. For this reason, success in stock enhancement will probably depend upon the simultaneous release of conch in numerous high-quality sites over more than one year.

(5) Predation-induced mortality in juvenile queen conch declines significantly with increasing conch density, at least up to the point at which growth is inhibited. The optimal density for conch releases is probably site-specific, but considerable "safety in numbers" occurs at approximately one conch per square meter. As yet, it is impossible to recommend how many conch should be released at any one site, but several thousand would appear to represent a minimum.

(6) Given the high mortality rates during summer, releases should be made in the fall concurrent with declining water temperature.

Natural mortality rates in juvenile queen conch are high and growth rates are relatively low (Stoner and Ray, 1993; Stoner and Davis, 1994). Therefore, stock-enhancement programs should be built upon realistic expectations of survivorship and yield. Given the current relatively high cost of producing seed conch and the relatively low price of conch as a fishery product (e.g., US\$1.00 per adult conch in the Bahamas), the direct enhancement of fisheries by release of hatchery-reared conch may not yet be economically fea-

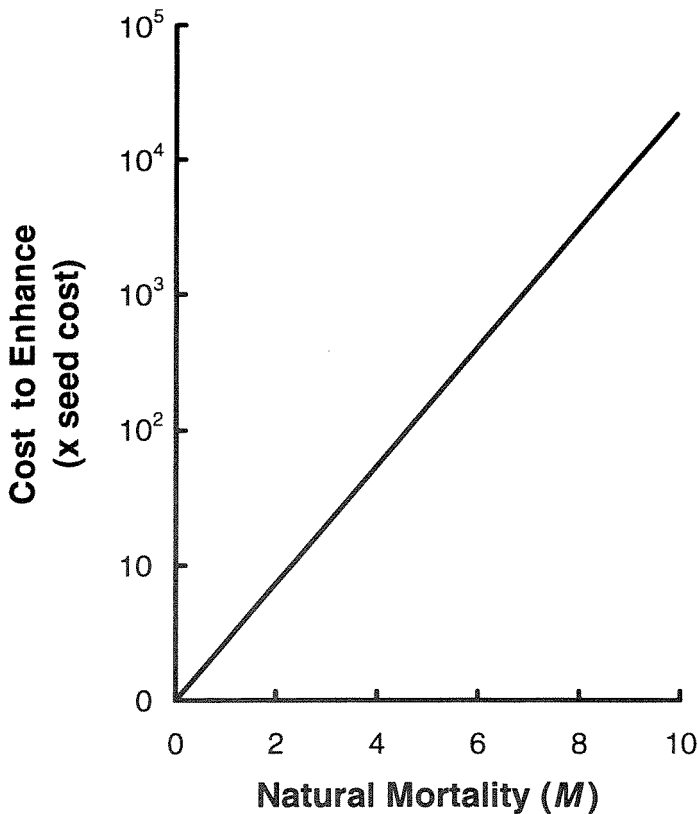


Figure 6. Theoretical relationship between instantaneous rate of natural mortality ( $M$ ) and cost to enhance. Here we define "cost to enhance" as the value of survivors relative to seed cost 1 yr after release. The cost of enhancement will increase logarithmically with increase in the rate of natural mortality.

sible. However, conch populations in many areas, including the United States, have been depleted to a level where they may not recover naturally (Stoner et al., 1996, 1997), and stock rehabilitation is the primary goal. In cases such as this, the value of conch surviving to adulthood may best be measured in terms of their reproductive potential rather than their direct contribution to stock numbers. Research in transgenerational enhancement may be particularly productive where populations have been severely reduced and fishing moratoria are in effect.

**IMPLICATIONS OF VARIATION IN MORTALITY.**—Rates of natural mortality are often calculated over relatively long periods of time for animals that are large and easy to tag and recapture. Data for small individuals, normally used in releases, are often rare. Among economically significant marine species, mortality rates are probably best studied for molluscs such as abalone (Shepherd and Breen, 1992) and scallops (Orensanz et al., 1991). We have extracted a sample of mortality data for various abalones, hard clam (*Mercenaria mercenaria*), and bay scallop (*Argopecten irradians*), with emphasis on the first year or two of life (Table 2). Values for  $M$  below 1.0 are uncommon, and the ranges tend to be

great, similar to our findings with queen conch. Magnitude and variation in mortality rates can have important consequences related to stock enhancement.

The cost to enhance a stock in the wild can be defined as:

$$\frac{(\text{cost of seed})(\text{number of seed released})}{(\text{number of individuals recovered})}$$

and (cost of seed)  $\cdot e^M$

Thus, cost of enhancement is a direct function of mortality (Fig. 6), and cost will rise logarithmically with  $M$ . For example, a mortality rate of at least 2.0 is common in queen conch (Fig. 2) and many other juvenile molluscs during the first year of life (Table 2). At this rate, cost to enhance is 7.39 times the initial seed cost 1 yr later (i.e.,  $e^2 = 7.39$ ). Although this might be an acceptable cost if seed are not expensive, a mortality rate of 7.0 results in a cost to enhance that is 1097 times the seed cost ( $e^7 = 1097$ ). Seed released at a cost of \$0.10 per individual would have values of \$0.74 and \$110.00 in the two scenarios, respectively. Many seed stocks cost considerably more than \$0.10.

The results of this investigation suggest that mortality rates in queen conch can be much higher than those predicted earlier. In addition to the relationship with conch size, mortality rates can be highly variable with season, habitat, conch density, and culture technique. Because of the logarithmic relationship between mortality rate and cost to enhance a stock, it is critical for those involved in stock enhancement to have a realistic understanding of mortality processes and effects and to optimize culture and release strategies that will help ensure high survival rates.

#### ACKNOWLEDGMENTS

Research in the Bahamas was supported by grants from the National Undersea Research Program of NOAA (U.S. Department of Commerce) and the Shearwater Foundation (New York). Many staff members at the Caribbean Marine Research Center, Vero Beach, Florida, assisted in the field work and analyses reported here: M. Davis, L. Hambrick, R. Jones, C. Kelso, J. Lally, S. O'Connell, M. Ray, V. Sandt, J. Thonney, J. Waite, and E. Wishinski. Research in Florida was supported by the Florida Department of Environmental Protection and the Partners for Wildlife grants program of the U.S. Fish and Wildlife Service (U.S. Department of the Interior). Many individuals participated in the Florida surveys and culture of conch, most notably L. Anderson, K. McCarthy, and R. Jones. The Nature Conservancy and M. Engstrom provided many volunteers for the surveys. M. Ray prepared the manuscript graphics and provided helpful criticism of the text.

#### LITERATURE CITED

- Appeldoorn, R. S. 1985. Growth, mortality, and dispersion of juvenile, laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. *Bull. Mar. Sci.* 37: 785–793.
- \_\_\_\_\_. 1988. Ontogenetic changes in natural mortality rate of queen conch, *Strombus gigas* (Mollusca: Mesogastropoda). *Bull. Mar. Sci.* 42: 159–165.
- \_\_\_\_\_. 1994. Queen conch management and research: status, needs and priorities. Pages 301–319 in R. S. Appeldoorn and B. Rodriguez, eds. *Queen conch biology, fisheries and mariculture*. Fundac. Cient. Los Roques, Caracas, Venezuela.
- Berg, C. J., Jr. 1976. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. *Mar. Biol.* 34: 191–199.

- \_\_\_\_\_ and R. A. Glazer. 1995. Stock assessment of a large marine gastropod (*Strombus gigas*) using randomized and stratified towed-diver censusing. ICES Mar. Sci. Symp. 199: 247–258.
- \_\_\_\_\_, J. Ward, B. Luckhurst, K. Nisbet and F. Cooper. 1992. Observations of breeding aggregations of the queen conch, *Strombus gigas*, in Bermuda. Proc. Gulf Carib. Fish. Inst. 42: 161–171.
- Berg, S. and J. Jorgensen. 1991. Stocking experiments with 0+ and 1+ trout parr, *Salmo trutta* L., of wild and hatchery origin: 1. Post-stocking mortality and smolt yield. J. Fish Biol. 39: 151–169.
- Creswell, L. R. 1994. An historical overview of queen conch mariculture. Pages 223–230 in R. S. Appeldoorn and B. Rodriguez, eds. Queen conch biology, fisheries and mariculture. Fundac. Cient. Los Roques, Caracas, Venezuela.
- Davis, M. 1994. Mariculture techniques for queen conch (*Strombus gigas* Linné): egg mass to juvenile stage. Pages 231–252 in R. S. Appeldoorn and B. Rodriguez, eds. Queen conch biology, fisheries and mariculture. Fundac. Cient. Los Roques, Caracas, Venezuela.
- \_\_\_\_\_, C. Hesse and G. Hodgkins. 1987. Commercial hatchery procedures for queen conch, *Strombus gigas*, seed for the research and grow-out market. Proc. Gulf Carib. Fish. Inst. 38: 326–335.
- Day, R. W. and A. E. Leorke. 1986. Abalone catches — what factors affect them. Aust. Fish. 45(10): 32–36.
- Emmett, B. and G. S. Jamieson. 1988. An experimental transplant of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, British Columbia. Fish. Bull., U.S. 87: 95–104.
- Flagg, P. J. and R. E. Malouf. 1983. Experimental plantings of juveniles of the hard clam *Mercenaria mercenaria* (Linné) in the waters of Long Island, New York. J. Shellfish Res. 3: 19–27.
- Glazer, R. A. and C. J. Berg, Jr. 1994. Current and future queen conch, *Strombus gigas*, research in Florida. Pages 79–95 in R. S. Appeldoorn and B. Rodriguez, eds. Queen conch biology, fisheries and mariculture. Fundac. Cient. Los Roques, Caracas, Venezuela.
- \_\_\_\_\_, K. J. McCarthy, R. L. Jones and L. Anderson. In press. The use of underwater metal detectors to locate outplants of the mobile marine gastropod, *Strombus gigas* L. Proc. Gulf Carib. Fish. Inst. 49.
- Iversen, E. S., D. E. Jory and S. P. Bannerot. 1986. Predation on queen conchs, *Strombus gigas*, in the Bahamas. Bull. Mar. Sci. 39: 61–75.
- Jackson, C. H. N. 1939. The analysis of an animal population. J. Anim. Ecol. 8: 238–246.
- Jory, D. E. 1982. Predation by tulip snails, *Fasciolaria tulipa*, on queen conchs, *Strombus gigas*. M.S. Thesis, University of Miami, Florida. 74 p.
- \_\_\_\_\_, and E. S. Iversen. 1983. Conch predators: not a roadblock to mariculture. Proc. Gulf Carib. Fish. Inst. 35: 108–111.
- Laughlin, R. A. and E. Weil. 1983. Queen conch mariculture and restoration in the Archipiélago de Los Roques. Proc. Gulf Carib. Fish. Inst. 35: 64–72.
- Marshall, L. S., Jr. 1992. Survival of juvenile queen conch, *Strombus gigas*, in natural habitats: impact of prey, predator, and habitat features. Ph.D. Dissertation, College of William and Mary, Virginia. 144 p.
- Martín-Mora, E., F. James and A. Stoner. 1995. Developmental plasticity in the shell of the queen conch, *Strombus gigas*. Ecology 76: 981–994.
- McShane, P. E. 1990. The fisheries ecology of Victorian abalone. Ph.D. Dissertation, La Trobe Univ., Melbourne, Australia (cited in Shepherd and Breen, 1992).
- Olla, B. L., M. W. Davis and C. H. Ryer. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquacult. Fish. Manage. 25 (Suppl. 1): 19–34.
- Orensanz, J. M., A. M. Parma and O. O. Iribane. 1991. Population dynamics and management of natural stocks. Pages 625–713 in S. E. Shumway, ed. Scallops: biology, ecology and aquaculture. Elsevier, Amsterdam.

- Peterson, C. H., H. C. Summerson and J. Huber. 1995. Replenishment of hard clam stocks using hatchery seed: combined importance of bottom type, seed type, planting season, and density. *J. Shellfish Res.* 14: 293–300.
- Randall, J. E. 1964. Contributions to the biology of the queen conch, *Strombus gigas*. *Bull. Mar. Sci. Gulf Carib.* 14: 246–295.
- Ray, M. and A. W. Stoner. 1994. Experimental analysis of growth and mortality in a marine gastropod aggregation: balancing growth with safety in numbers. *Mar. Ecol. Prog. Ser.* 105: 47–59.
- \_\_\_\_\_. 1995a. Growth, survivorship, and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. *Mar. Ecol. Prog. Ser.* 123: 83–94.
- \_\_\_\_\_. 1995b. Predation on a tropical spinose gastropod: the role of shell morphology. *J. Exp. Mar. Biol. Ecol.* 187: 207–222.
- \_\_\_\_\_, A. W. Stoner and S. M. O'Connell. 1994. Size-specific predation of juvenile queen conch, *Strombus gigas*: implications for stock enhancement. *Aquaculture* 128: 79–88.
- \_\_\_\_\_, M. Davis and A. W. Stoner. In review. Escaping the xanthid crab gauntlet—the role of size, density and habitat for a newly-settled gastropod. *J. Exp. Mar. Biol. Ecol.*
- Saito, K. 1984. Ocean ranching of abalones and scallops in northern Japan. *Aquaculture* 39: 361–373.
- Sandt, V. J. and A. W. Stoner. 1993. Ontogenetic shift in habitat by early juvenile queen conch, *Strombus gigas*: patterns and potential mechanisms. *Fish. Bull., U.S.* 91: 516–525.
- Schiel, D. R. 1992. The enhancement of paua (*Haliotis iris* Martyn) populations in New Zealand. Pages 474–484 in S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Prío, eds. *Abalone of the world: biology, fisheries and culture*. Fishing News Books, Oxford, UK.
- \_\_\_\_\_. 1993. Experimental evaluation of commercial-scale enhancement of abalone *Haliotis iris* populations in New Zealand. *Mar. Ecol. Prog. Ser.* 97: 167–181.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed., Charles Griffen & Co. London. 654 p.
- Shepherd, S. A. 1987. Aspects of the biology of the abalone *Haliotis laevis* and *Haliotis scalaris*. Ph.D. Thesis, Deakin University, Australia (cited in Shepherd and Breen, 1992).
- \_\_\_\_\_, and P. A. Breen. 1992. Mortality in abalone: its estimation, variability and causes. Pages 276–304 in S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Prío, eds. *Abalone of the world: biology, fisheries and culture*. Fishing News Books, Oxford, UK.
- \_\_\_\_\_, and C. Godoy. 1989. Studies on southern Australian abalone (genus *Haliotis*). XI. Movement and natural mortality of juveniles. *J. Malacol. Soc. Aust.* 10: 87–95.
- Stoner, A. W. 1994. Significance of habitat and stock pre-testing for enhancement of natural fisheries: experimental analyses with queen conch. *J. World Aquacult. Soc.* 25: 402–424.
- \_\_\_\_\_, and M. Davis. 1994. Experimental outplanting of juvenile queen conch, *Strombus gigas*: comparison of wild and hatchery-reared stocks. *Fish. Bull., U.S.* 92: 390–411.
- \_\_\_\_\_, and J. Lally. 1994. High-density aggregation of queen conch, *Strombus gigas*: formation, patterns, and ecological significance. *Mar. Ecol. Prog. Ser.* 106: 73–84.
- \_\_\_\_\_, and M. Ray. 1993. Aggregation dynamics in juvenile queen conch: population structure, growth, mortality, and migration. *Mar. Biol.* 116: 571–582.
- \_\_\_\_\_, M. D. Hanisak, N. P. Smith and R. A. Armstrong. 1994. Large-scale distribution of queen conch nursery habitats: implications for stock enhancement. Pages 169–189 in R. S. Appeldoorn and B. Rodriguez, eds. *Queen conch biology, fisheries and mariculture*. Fundac. Cient. Los Roques, Caracas, Venezuela.
- \_\_\_\_\_, R. A. Glazer and P. J. Barile. 1996. Larval supply to queen conch nurseries: relationships with recruitment process and population size. *J. Shellfish Res.* 15: 407–420.
- \_\_\_\_\_, N. Mehta and T. N. Lee. 1997. Recruitment of *Strombus* veligers to the Florida Keys reef tract: relation to hydrographic events. *J. Shellfish Res.* 16: 1–6.

- Tettelbach, S. T. and P. Wenczel. 1993. Reseeding efforts and the status of bay scallop *Argopecten irradians* (Lamarck, 1819) populations in New York following the occurrence of "brown tide" algal blooms. *J. Shellfish Res.* 12: 423–431.
- Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. *Fish. Bull., U.S.* 86: 25–43.
- Weil, E. and R. Laughlin. 1984. Biology, population dynamics, and reproduction of the queen conch, *Strombus gigas* Linné, in the Archipiélago de Los Roques National Park. *J. Shellfish Res.* 4: 45–62.
- Whetstone, J. M. and A. G. Eversole. 1978. Predation on hard clams *Mercenaria mercenaria* by mud crabs *Panopeus herbstii*. *Proc. Natl. Shellfish Assoc.* 68: 42–48.

DATE ACCEPTED: September 2, 1997.

ADDRESSES: (A.W.S.) *National Marine Fisheries Service, Northeast Fisheries Science Center, 74 Magruder Road, Highlands, New Jersey 07723*; (R.A.G.) *Florida Marine Research Institute, Department of Environmental Protection, 2796 Overseas Highway, Suite 119, Marathon, Florida 33050*.